DOI:
10.1016/S0925-2312(02)00847-0

Document Version
Peer reviewed version

Neurocomputing, 52-54:389–95, 2003.

Exploring the Functional Significance of Dendritic Inhibition In Cortical Pyramidal Cells

M. W. Spratling and M. H. Johnson
Centre for Brain and Cognitive Development, Birkbeck College, London. UK.

Abstract

Inhibitory synapses contacting the soma and axon initial segment are commonly presumed to participate in shaping the response properties of cortical pyramidal cells. Such an inhibitory mechanism has been explored in numerous computational models. However, the majority of inhibitory synapses target the dendrites of pyramidal cells, and recent physiological data suggests that this dendritic inhibition affects tuning properties. We describe a model that can be used to investigate the role of dendritic inhibition in the competition between neurons. With this model we demonstrate that dendritic inhibition significantly enhances the computational and representational properties of neural networks.

Keywords: Dendrites, inhibition, competition, receptive fields, learning.

1 Introduction

Lateral inhibition between cortical cells is known to play an important role in determining the receptive field properties of those cells (Eysel et al., 1998; Jagadeesh, 2000). Such lateral inhibition provides a mechanism through which neurons compete to respond to the current pattern of stimulation. The vast majority (93%) of inhibitory synapses targeting neocortical pyramidal cells terminate on the dendrites (DeFelipe and Fariñas, 1992; Fiala and Harris, 1999). This dendritic inhibition is likely to have strong effects only on more distal inputs along the same dendritic branch (Borg-Graham et al., 1998; Koch et al., 1983; Koch and Segev, 2000; Rall, 1964; Segev, 1995; Spruston et al., 1999), and will thus selectively inhibit specific groups of excitatory inputs, or dendritic compartments. In contrast, many neural network models assume that dendrites have passive conductance properties (Mel, 1999), and hence, that all inhibitory contacts are equally effective at suppressing responses to any excitatory inputs. For such point-neuron models, all inhibitory contacts act as if they target the soma or axon initial segment.

While somatic inhibition non-selectively inhibits responses to all stimuli, dendritic inhibition selectively inhibits specific patterns of excitatory inputs. Recent physiological data suggests that the latter mechanism is important in determining the response properties of cortical pyramidal cells since the blockade of GABAergic synapses (in monkey area TE) results in specific dis-inhibition of responses to particular stimulus features rather than removal of non-specific inhibition (Wang et al., 2000). We propose a simple neural network architecture which can be used to explore the role of dendritic inhibition as a mechanism of competition between pyramidal cells.

2 Method

Figure 1(a) illustrates the architecture used by conventional models of lateral inhibition. In some implementations, competition is achieved (as shown) by using explicit lateral connections between the nodes (von der Malsburg, 1973; Földiák, 1990; Marshall, 1995), while in others, competition is implemented implicitly through a selection process which chooses the 'winning' node(s) (Rumelhart and Zipser, 1985; Kohonen, 1997; Grossberg, 1987). In all of these algorithms, nodes attempt to 'block' other nodes from generating a response to the current stimulus. A node's success in this competition is dependent on the total strength of the stimulation it receives and nodes which compete unsuccessfully have their output activity suppressed.

Figure 1(b) shows the architecture of our model of dendritic inhibition. As with conventional models, we simplify reality by assuming that the role of interneurons can be approximated by direct inhibitory connections between excitatory nodes. Furthermore, we group together all the synapses contributing to a dendritic compartment to form a single input to the node. Dendritic inhibition is then modeled as (linear) inhibition of this input. This mechanism thus enables nodes to selectively inhibit other nodes from responding to particular input features. Full details of this algorithm can be found in (Spratling and Johnson, 2002)

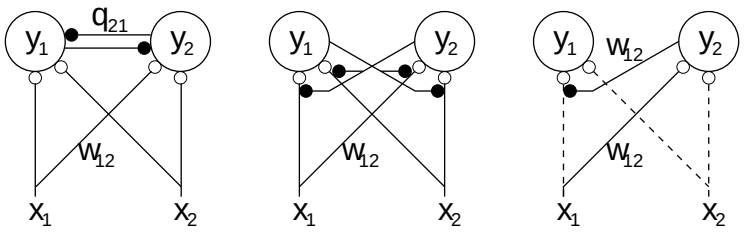

Figure 1: Mechanisms of lateral inhibition. Simple, two-node, networks are presented to illustrate different mechanisms of lateral inhibition. Nodes are shown as large circles, excitatory synapses as small open circles, and inhibitory synapses as small filled circles. (a) The conventional model of lateral inhibition provides competition between node outputs. (b) Dendritic inhibition provides competition for inputs. (c) For the simulations presented here, each lateral weight (such as the one shown) has a strength that is equal to the corresponding afferent weights (shown as a solid line for this example).

3 Results

By making the lateral weights equal in strength to the corresponding afferent weights (as shown in figure 1(c)) each node can 'block' its preferred inputs from activating other nodes. With this arrangement of weights, if a node is strongly activated by the stimulus, and it has a strong synaptic weight to a certain feature of that stimulus, then it will inhibit other nodes from responding to that feature. On the other hand, if an active node receives a weak synapse from a certain input, then it will weakly inhibit other nodes from responding to that specific input. Hence, if individual nodes have learnt weights that are selective to certain stimuli then when multiple stimuli are simultaneously presented to the network each of the nodes representing one of these stimuli can be simultaneously active. A network using dendritic inhibition can thus respond appropriately to any combination of input patterns. Furthermore, such a network deals naturally with stimuli which share sub-features in common (*i.e.*, patterns which overlap in the input space). This capacity is important if different sets of neurons are to respond to distinct sensory events which may share many features in common. Both these properties are illustrated in figure 2. In this example six nodes each represent one of six patterns defined across six input features (labelled 'a' to 'f'). Each node responds exclusively to its preferred input pattern despite the strong overlap between stimuli. Furthermore, multiple nodes responds when multiple stimuli are presented.

Competition not only makes responses more selective (in the short-term), but since learning is activity-dependent it also makes the receptive fields of individual nodes more distinct (in the long-term). Improved response properties result in more correct learning episodes (Marshall, 1995), and hence, the advantageous coding properties that arise from using dendritic inhibition can result in efficient, unsupervised, learning (Spratling and Johnson, 2002). For example, figure 3(b) shows the performance of our algorithm when applied to the bars problem (Földiák, 1990). Corresponding results for a conventional neural network architecture are shown in figure 3(c). The speed of learning when using dendritic inhibition compares favourably, not only to networks that use the conventional form of lateral inhibition, but with all neural network algorithms that have been applied to this task (Spratling and Johnson, 2002). More significantly, a single algorithm can learn to represent the independent components of the training data (*i.e.*, the individual bars) under a number of different conditions (such as the number of nodes in the network, the frequency with which bars appear and the number of bars making up each image). In contrast, a conventional network architecture requires *a priori* information about the task in order to define learning rules that will find appropriate weights for a particular task. For example, to solve the bars problem, Földiák (Földiák, 1990) found it is necessary to use the value for the probability of a bar being active within the learning rules. Hence, this algorithm fails to learn even when the statistics of the input data are only slightly different from that expected (as illustrated in figure 3(c)). Furthermore, even with *a priori* knowledge of each task, it would not be possible to define appropriate learning rules for each case. Algorithms which use the conventional mechanism of lateral inhibition are thus severely restricted in the class of problems that they can successfully learn, and require *a priori* knowledge to succeed even on those tasks.

4 Conclusion

A network of neurons competing through dendritic lateral inhibition is capable of generating correct representations based on the 'knowledge' stored in the synaptic weights of the neurons. Specifically, it is capable of generating a local encoding of individual input patterns as well as responding simultaneously to multiple patterns,

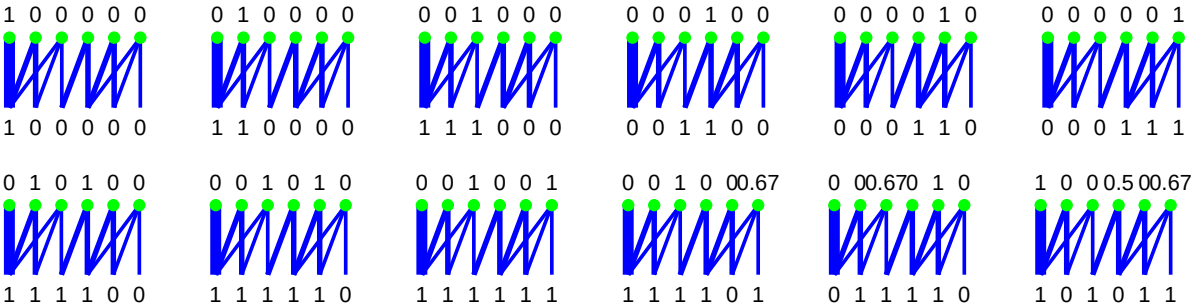

Figure 2: Representing multiple, overlapping, input patterns. A network consisting of six nodes receiving six inputs ('a', 'b', 'c', 'd', 'e', and 'f') is wired up so that nodes are selective to the patterns 'a', 'ab', 'abc', 'cd', 'de', and 'def'. The response of the network to each of these input patterns is shown on the top row. Dendritic inhibition (lateral weights have been omitted from the figures) enables each node to respond exclusively to its preferred pattern. In addition, the response to multiple and partial patterns is shown on the bottom row. Pattern 'abcd' causes the nodes representing 'ab' and 'cd' to be active simultaneously, despite the fact that this pattern overlaps strongly with pattern 'abc'. Input 'abcde' is parsed as 'abc' together with 'de', and input 'abcdef' is parsed as 'abc' + 'def'. Input 'abcdf' is parsed as 'abc' + two-thirds of 'def', hence the addition of 'f' to the pattern 'abcd' radically changes the representation that is generated. Input 'bcde' is parsed as two-thirds of 'abc' plus pattern 'de'. Input 'acef' is parsed as 'a' + one half of 'cd' + two-thirds of pattern 'def'.

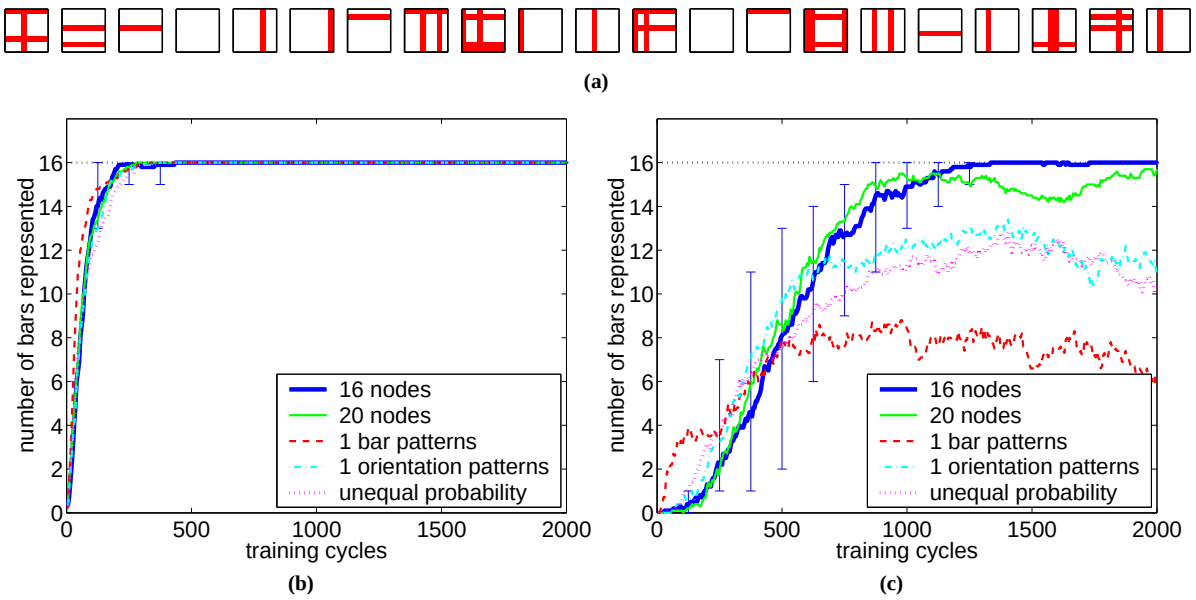

Figure 3: The bars problem. (a) Examples of typical input patterns used in the bars problem. Bars in an 8x8 pixel image are active with probability $\frac{1}{8}$. Dark pixels indicate active inputs. The speed of learning is illustrated for (b) our algorithm, and (c) Földiák's algorithm (Földiák, 1990). Each plot shows the change, over the course of training, in the number of bars correctly represented by exactly one node in the neural network. Mean performance, over ten trials (using different randomly generated sequences of training patterns) is shown. Performance is plotted for networks containing 16 and 20 nodes trained with the standard bars data (like that illustrated in (a)), and for 16-node networks trained with images each containing a single bar, with images which contained only horizontal or only vertical bars, and with images in which horizontal bars occurred with half the probability of vertical bars. For each of these variations the dendritic inhibition model learns reliably and quickly, while the model using the conventional mechanism for lateral inhibition fails to learn any of the tasks except the standard bars problem for which it was specifically designed. The error bars show the best and worst performance over all trials for a 16-node network trained on the standard bars problem.

when they are present, in order to generate a distributed encoding. It can produce an appropriate representation even when patterns overlap and respond to partial patterns such that the response is proportional to how well that input matches the stored pattern. Not only can dendritic inhibition provide appropriate coding properties, it can also be used to efficiently learn such representations. Hence, competition via dendritic inhibition significantly enhances the computational and representational capacities of networks of neurons and may be exploited by cortical circuits. Furthermore, such a neural network has significant practical advantages over algorithms that employ the conventional mechanism of competition.

Our architecture assumes that all afferent synapses, carrying information about a feature of the input space, can be modelled as a single input to a node. This can be justified since it is presumed that related synapses cluster together within dendritic trees so that local operations are performed by multiple, functionally distinct, dendritic subunits before integration at the soma (Koch and Segev, 2000; Segev and Rall, 1998; Segev, 1995; Häusser et al., 2000; Häusser, 2001; Mel, 1994, 1999). Dendritic inhibition could thus act to 'block' the output from individual functional compartments. It has long been recognized that a dendrite composed of multiple subunits would provide a significant enhancement to the computational powers of an individual neuron (Mel, 1994, 1999) and that dendritic inhibition could contribute to this enhancement (Koch et al., 1983; Koch and Segev, 2000; Segev and Rall, 1998). However, the role of dendritic inhibition in competition between cells and its subsequent effect on neural coding and receptive field properties has not previously been investigated.

The idea embodied in our model is that pyramidal cells inhibit the activity of dendritic compartments in other pyramidal cells within the same cortical area. It has been shown that cortical pyramidal cells innervate inhibitory cell types which in turn form synapses on the dendrites of pyramidal cells (Buhl et al., 1997; Tamas et al., 1997). Our model predicts that it should be possible to find pairs of pyramidal cells for which action potentials generated by one cell induce inhibitory post-synaptic potentials within the dendrites of the other. More complex models, which include a separate inhibitory cell population, and which use multi-compartmental models of dendritic processes could relate our proposal more directly with physiology. We hope that our demonstration of the computational and representational advantages that could arise from dendritic inhibition will serve to stimulate more detailed studies of this type.

Acknowledgements

This work was funded by MRC Research Fellowship number G81/512.

References

L. T. Borg-Graham, C. Monier, and Y. Fregnac. Visual input evokes transient and strong shunting inhibition in visual cortical neurons. *Nature*, 393(6683):369–73, 1998.

E. H. Buhl, G. Tamas, T. Szilagyi, C. Stricker, O. Paulsen, and P. Somogyi. Effect, number and location of synapses made by single pyramidal cells onto aspiny interneurones of cat visual cortex. *The Journal of Physiology,*, 500 (3):689–713, 1997.

J. DeFelipe and I. Fariñas. The pyramidal neuron of the cerebral cortex: morphological and chemical characteristics of the synaptic inputs. *Progress in Neurobiology*, 39(6):563–607, 1992.

U. T. Eysel, I. A. Shevelev, N. A. Lazareva, and G. A. Sharev. Orientation tuning and receptive field structure in cat striate neurons during local blockade of intrcortical inhibition. *Neuroscience*, 84(1):25–36, 1998.

J. Fiala and K. Harris. Dendritic structure and spines. In G. Stuart, N. Spruston, and M. Häusser, editors, *Dendrites*, chapter 1, pages 1–34. Oxford University Press, Oxford, UK, 1999.

P. Földiák. Forming sparse representations by local anti-Hebbian learning. *Biological Cybernetics*, 64:165–70, 1990.

S. Grossberg. Competitive learning: from interactive activation to adaptive resonance. *Cognitive Science*, 11: 23–63, 1987.

M. Häusser. Synaptic function: dendritic democracy. *Current Biology*, 11(1):R10–2, 2001.

M. Häusser, N. Spruston, and G. J. Stuart. Diversity and dynamics of dendritic signalling. *Science*, 290(5492): 739–44, 2000.

B. Jagadeesh. Inhibition in inferotemporal cortex: generating selectivity for object features. *Nature Neuroscience*, 3(8):749–50, 2000.

C. Koch, T. Poggio, and V. Torre. Nonlinear interactions in a dendritic tree: localization, timing, and role in information processing. *Proceedings of the National Academy of Sciences USA*, 80(9):2799–802, 1983.

C. Koch and I. Segev. The role of single neurons in information processing. *Nature Neuroscience*, 3(supplement): 1171–7, 2000.

T. Kohonen. *Self-Organizing Maps*. Springer-Verlag, Berlin, 1997.

J. A. Marshall. Adaptive perceptual pattern recognition by self-organizing neural networks: context, uncertainty, multiplicity, and scale. *Neural Networks*, 8(3):335–62, 1995.

B. W. Mel. Information processing in dendritic trees. *Neural Computation*, 6:1031–85, 1994.

B. W. Mel. Why have dendrites? A computational perspective. In G. Stuart, N. Spruston, and M. Häusser, editors, *Dendrites*, chapter 11, pages 271–89. Oxford University Press, Oxford, UK, 1999.

W. Rall. Theoretical significance of dendritic trees for neuronal input-output relations. In R. F. Reiss, editor, *Neural Theory and Modeling*, pages 73–97. Stanford University Press, Stanford, CA, 1964.

D. E. Rumelhart and D. Zipser. Feature discovery by competitive learning. *Cognitive Science*, 9:75–112, 1985.

I. Segev. Dendritic processing. In M. A. Arbib, editor, *The Handbook of Brain Theory and Neural Networks*, pages 282–9. MIT Press, Cambridge, MA, 1995.

I. Segev and W. Rall. Excitable dendrites and spines: earlier theoretical insights elucidate recent direct observations. *Trends in Neurosciences*, 21(11):453–60, 1998.

M. W. Spratling and M. H. Johnson. Pre-integration lateral inhibition enhances unsupervised learning. *Neural Computation*, 14(9):2157–79, 2002.

N. Spruston, G. Stuart, and M. Häusser. Dendritic integration. In G. Stuart, N. Spruston, and M. Häusser, editors, *Dendrites*, chapter 10, pages 231–271. Oxford University Press, Oxford, UK, 1999.

G. Tamas, E. H. Buhl, and P. Somogyi. Fast IPSPs elicited via multiple synaptic release sites by different types of GABAergic neurone in the cat visual cortex. *The Journal of Physiology,*, 500(3):715–38, 1997.

C. von der Malsburg. Self-organisation of orientation sensitive cells in the striate cortex. *Kybernetik*, 14:85–100, 1973.

Y. Wang, I. Fujita, and Y. Murayama. Neuronal mechanisms of selectivity for object features revealed by blocking inhibition in inferotemporal cortex. *Nature Neuroscience*, 3(8):807–13, 2000.